

Habitat preferences of hazel dormice *Muscardinus avellanarius* and the effects of tree-felling on their movement

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ABSTRACT

Modern management of multifunctional woodlands must address many and various demands, including for recreation, timber production and the conservation of biodiversity. The responses of individuals and populations of protected species to woodland management and habitat change are often not well understood. Using radio-tracking and LiDAR, we investigated the short-term habitat preferences of hazel dormice *Muscardinus avellanarius*, and their ranging and resting behaviours before and after small-scale tree felling, following a before-after control-impact design. Mean dormouse home range size was 0.51 Ha (± 0.07 SE, $n = 16$) and did not vary between sexes or among sites, though heavier animals had smaller ranges. Dormice preferred mid-height woodland habitat (5–10 m tall), with low proportions of high forest (over 10 m tall), for both ranging and resting sites. Ranging habitats were often located on woodland edges and relatively dense vegetation. Dormice preferentially used yew, rowan and hazel during ranging. There was no difference in the distances travelled by dormice before and after felling, but dormice in areas where trees had been felled showed less evidence of a shift in ranging area than those in unfelled areas. Although the limited response of dormice to tree felling activities has the potential to be associated with increased mortality and/or limited dispersal of individual dormice, the requirements of dormice for mid-successional and edge habitats that arise after tree removal means that a dynamic optimum of felling and regeneration is essential for conservation of dormouse populations.

1. Introduction

Woodlands are increasingly required to fulfil multiple functions including recreation, conservation and the production of timber and other forest products (Pimental et al., 1992; Schulz et al., 2014). Realising these multiple objectives often involves woodland management activities such as harvesting, thinning, coppicing or ride and glade maintenance (Quine et al., 2011). However, woodlands are often home to protected and threatened species that may be adversely affected, whether individually or collectively, directly or indirectly, by management activities (Lindenmayer, 1999). These species are often protected by national and international legislation, making it a legal imperative for private and public woodland owners, and in some cases statutory authorities, to reduce or mitigate actual or potential harm caused by forestry activities (Young et al., 2005). This can have major consequences for forestry and woodland management, and substantial resources are dedicated to addressing protective legislation in

developing forest management practice (Nalle et al., 2004). The responses of protected species to tree removal are frequently not as well understood as might be desired, both in relation to short-term effects on individuals and longer-term, or larger-scale, effects on population dynamics (Blumstein, 2010). Likely effects are therefore often assumed and general mitigation measures are applied (Reinert et al., 2011). Understanding how protected species use their woodland habitats and react to silvicultural and other habitat management activities is therefore key to designing management plans and employing resources most efficiently (Cook et al., 2017).

The hazel dormouse *Muscardinus avellanarius* is a European Protected Species, listed under Annex IV of the European Habitats Directive (1992), and the UK Habitats Regulations (1994 and 2010). Dormouse populations in the United Kingdom have undergone declines of 72% (62–79%, 95% confidence intervals) from 1993 to 2014 (Goodwin et al., 2017). This decline has been attributed to changes in climate, and woodland habitat configuration and quality (Goodwin

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Table 1

Summary of vegetation structure at study sites in Central Kent and South Devon. Measures are means taken from all sampling points, i.e. those used by and available to dormice. Mean SD of vegetation height is the mean standard deviation in a 3 m x 3 m sliding window (see Methods).

Site	Mean vegetation height (m)	Mean SD of vegetation height (m)	Mean canopy density	% under 1 m	% 1–2 m	% 2–5 m	% 5–10 m	% over 10 m
Central Kent	8.34	1.88	0.62	4.56	3.48	17.54	37.58	36.84
South Devon	9.71	1.95	0.60	10.10	3.82	10.51	32.27	43.31

et al., 2018). The hazel dormouse is an arboreal species, inhabiting woodland, forest and scrub areas and has often been associated with successional wooded habitats (Becker and Encarnação, 2015; Bright and Morris, 1990; Juškaitis, 2007). It therefore exemplifies the problems posed by being obliged to conserve a species by using protection at the level of the individual, in a system that is subject to frequent management and alteration of habitats. This problem is especially pertinent to dormice, as they are also likely to require active management to maintain their favoured habitats and thereby facilitate population persistence (Sozio et al., 2016; Goodwin et al., 2018). Studies have shown that the management of woodland habitats increases the survival and body condition of dormice within those habitats (Sozio et al., 2016), and populations across whole woodlands are resilient when management has taken place in parts of the woodland (Juškaitis, 2008; Trout et al., 2012). Studies of many woodlands across the UK have shown that populations respond positively to woodland management (Goodwin et al., 2018). Knowledge of the response of individual dormice to silvicultural activities, best exemplified by tree felling, is therefore needed in order to be able to start balancing any potential short-term effect on individuals with the longer-term conservation requirements of dormouse populations.

Most studies of the effect of forest management on small mammals have compared communities of small mammals in managed stands of forest to those in old growth forest (Carey and Harrington, 2001; Fauteux et al., 2012; Lindenmayer, 1999; Zwolak, 2009). However, this approach does not separate the proximate effects of forestry on populations (survival, emigration, changes in range use) from longer term habitat changes (Escobar et al., 2015). It is therefore important to examine the immediate behavioural and ecological responses of individuals to woodland management.

Dormice have been shown to occur in greater numbers, with increased survival and breeding success, in woodland vegetation of medium heights or with a developed understorey, and successional and scrubby habitats (Capizzi et al., 2002; Juškaitis and Šiožinyte, 2008; Sozio et al., 2016). Survey methods used in these studies capture broad habitat associations, often of resting sites (Goodwin et al., 2018), whereas telemetry can fine-tune conservation recommendations for the provision of habitats required for different activities, such as resting and ranging (Bright and Morris, 1992), as well as investigation of behavioural responses to changes in their environment (Doerr and Doerr, 2005). Remote sensing data now also make it possible to look at the selection of different vegetation structures (Garabedian et al., 2017), which are important for a variety of arboreal mammals (Berry et al., 2016; Falconi et al., 2015; Linnell et al., 2017; van der Ree and Bennett, 2003; Wilson et al., 2007). Understanding the preferences of animals can aid in predicting the likely effect of changes in vegetation structures, e.g. through tree removal and woodland management (Eyre et al., 2010).

We explored the ranging behaviour and preferences for tree species and vegetation structure shown by hazel dormice in two woodlands in England. We investigated the effects of tree felling within the ranges of dormice on both these sites. We tracked dormice before, during and after tree felling occurred, as well as in control areas of the sites, where no tree felling was carried out.

2. Materials and methods

2.1. Study sites

The study was conducted in two mixed broadleaf and conifer sites, in south Devon (SX813892) and central Kent (TQ530374) in England. The sites were selected as they had established and well-known dormouse populations, varied woodland habitat and were conducting ongoing tree felling activities. The two sites have similar ecological histories and management regimes and are both being converted from commercial conifer plantation to a mix of semi-natural broadleaved woodland, shrub and heath. Both sites have watercourses running through them and areas of wet woodland. The vegetation structures were similar between sites, with the major difference being that vegetation heights were slightly higher and there was a higher proportion of open ground on the South Devon site (Table 1). The vegetation species composition was slightly different between sites, however two of the three most abundant species groups on both sites were birch *Betula* spp., occurring in all of the dormouse ranges studied, and various conifer species, occurring in 96% of ranges. Sweet chestnut *Castanea sativa*, oak *Quercus* spp. and honeysuckle *Lonicera periclymenum* were also one of the 10 most abundant species at both sites. The identity of the other most abundant species in the areas differed. In Kent, buckthorn *Rhamnus cathartica*, *Rhododendron* spp., bramble *Rubus fruticosus* and yew *Taxus baccata* were found within between 30 and 50% of all the dormouse ranges, whereas they were absent in Devon. Whereas hazel *Corylus avellana* and cherry *Prunus* spp. were reasonably abundant within the areas studied in Devon but not recorded in Kent.

2.2. Tracking methodology and felling protocol

Dormice were captured during surveys of nest boxes that had previously been deployed for dormice. VHF radiocollars of between 0.8 and 1.1 g (3–6% of dormouse weight) were fitted to 20 dormice. 9 dormice were in areas of the sites in which trees would be felled, and 11 in control areas where no trees would be felled. The sex and weights of dormice were noted during collar fitting. The study was undertaken under licence from Natural England and the Home Office and with approval from the University of Exeter Animal Welfare and Ethical Review Board. Prior to deployment in the field, a video assessment was made of the night-time activity of two captive zoo dormice wearing dummy collars and no changes to movements were observed; other studies have similarly reported no discernible impediment to dormice from radiocollars (Bright and Morris, 1990).

Radiotracking was conducted between 29th September and 21st October 2015, as this time is often when felling or woodland management activities are carried out and when dormice are not often torpid during the day. Most location fixes were made by directly locating the animal to a specific tree or canopy area and recording the location with a handheld GPS device. Due to inaccessibility (steep slope, river) some location fixes were obtained via triangulation, from a mean distance of 28 m from bearings taken at two fixed points marked with a handheld GPS. A daytime fix was taken for each dormouse to record resting locations. Due to different numbers and locations of dormice on the two sites, nighttime sampling rates varied; an average of 3.8–5.3 fixes per 24-h period were taken for each dormouse in Devon, and 2.4–3.0 fixes in Kent. Fixes were not taken within one hour of each other to reduce

spatial autocorrelation of recordings. The time at which individuals were located was rotated to ensure comprehensive coverage of each animal over the active period (Fieberg, 2007; Fieberg and Börger, 2012).

Dormice were tracked for a period of days before and after tree felling was conducted following a Before-After-Control-Impact (BACI) design. Tree felling took place 5–7 days after tracking had begun and dormice were tracked for 8–11 days following felling. Trees were removed from 3 areas on the Devon site and 2 on the Kent site. The mean size of felled areas was 0.1 ha (0.06 ha SE). All dormice in felling areas were located in nestboxes situated from 0 m to 100 m from felling operations when trees were being felled. The mean distance was 38.6 m (10.7 m SE) and 6 dormice were in areas where trees adjacent to the nest box were felled. On these days in felling areas, the daytime locations of dormice were recorded on two additional occasions: once prior to the start of felling operations and once after operations had ended. Felling measures were similar on both sites, in that they consisted of clearing small areas of conifer, or mixed conifer and broadleaf trees, to create glades. The main difference was that a larger area of mostly conifer was removed on the South Devon site, compared to the site in Kent (Fig. 2).

2.3. Habitat data collection

The species of tree or shrub in which each dormouse was located was recorded. Conifer species were grouped, as were willow species, to ensure consistency in species classification. Data on the availability of tree species in the range of each dormouse were collected around a central point of its range, identified from radio-tracking; four 50 m transects were walked on North, South, East and West compass directions and all trees or shrubs > 1 m high within 1 m of the transect were recorded.

Light Detection and Ranging (LiDAR) data were used to assess vegetation structures. LiDAR measures canopy height from above at a fine

scale, and is used here to derive measures of canopy height and density, as well as spatial heterogeneity in structure. These canopy metrics will also reflect, to some extent, variation in the amount of light penetrating the canopy and so might act as a proxy for productivity and vegetation density below the canopy. Such remotely sensed data are powerful in that they are available at fine scale across large areas of woodland, and can be more consistent than terrestrial surveys. However, measures of height at the canopy clearly cannot capture all understorey characteristics, the implications of which may vary among tree species. The implications of using LiDAR data are discussed further below. Digital Surface Models (DSMs) and Digital Terrain Models (DTMs) were acquired from BlueSky International for 2014 for the Kent site, and from the Tellus project for 2013 the Devon site. DTMs were subtracted from DSMs to obtain vegetation heights. Data was resampled to 1 m resolution for BlueSky data (original resolution of 50 cm), using average values, making the datasets comparable. See Fig. 1 for examples.

2.4. Space-use analysis

To describe the dormouse ranges, we calculated Kernel Density Estimates (KDEs) from radio-tracking locations (Fieberg, 2007; Laver and Kelly, 2008). Ranges based on a standard time period of 13 days were used to enable equivalent comparisons of space use. Asymptotes in range sizes were reached over the 13-day period by individual dormice (Appendix A) and ranges estimated over a standardised number of days have been shown to be robust (Börger et al., 2006; Fieberg and Börger, 2012; Kochanny et al., 2009). Asymptotic distributions were investigated to look at estimated range size, and 95% Confidence Intervals (calculated from 1000 bootstrap samples), with increasing sample size (Calabrese et al., 2016; Laver and Kelly, 2008). Temporal autocorrelation was investigated using the R package ctm (Calabrese et al., 2016). KDEs were calculated using H-plugin smoothing bandwidth selection, as this did not over-smooth the data and is suitable for small sample sizes and animals with partially clumped space use

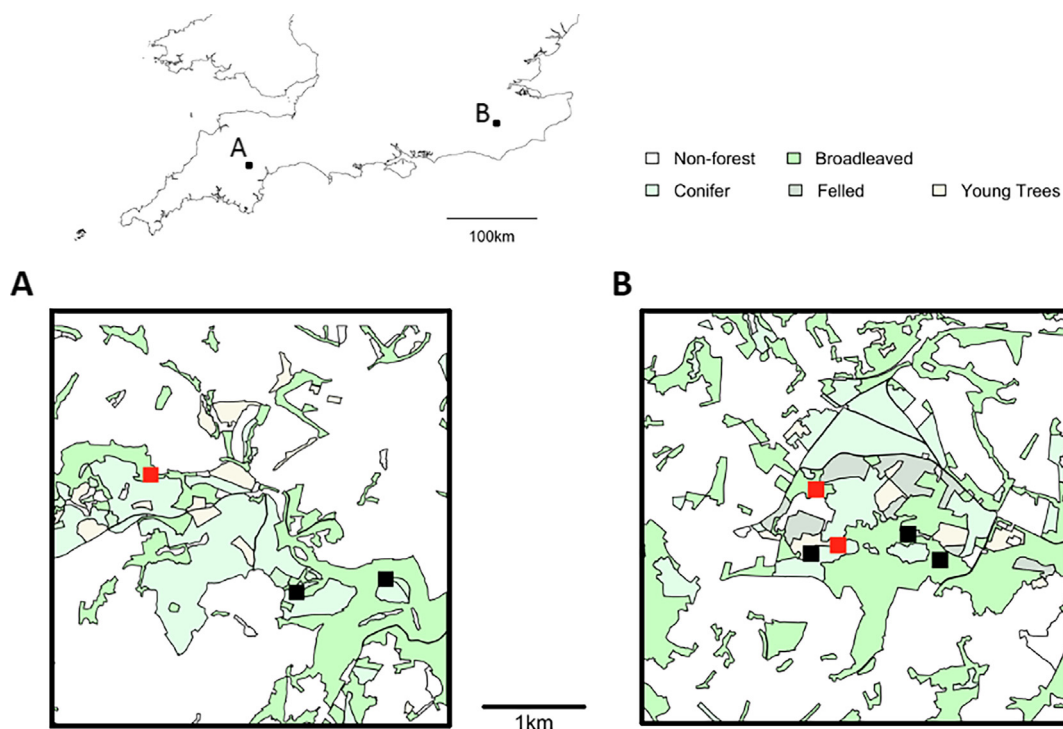


Fig. 1. Locations of the two sites at which dormice were radio-tracked and details of the distribution and composition of woodland habitats in the surrounding landscapes. Site A is in south Devon and B is in central Kent. Woodland habitat categories are from the National Forest Inventory 2015. The area in which dormice were tracked and where felling was conducted are shown as red squares and the control areas in which dormice were tracked are shown as black squares. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

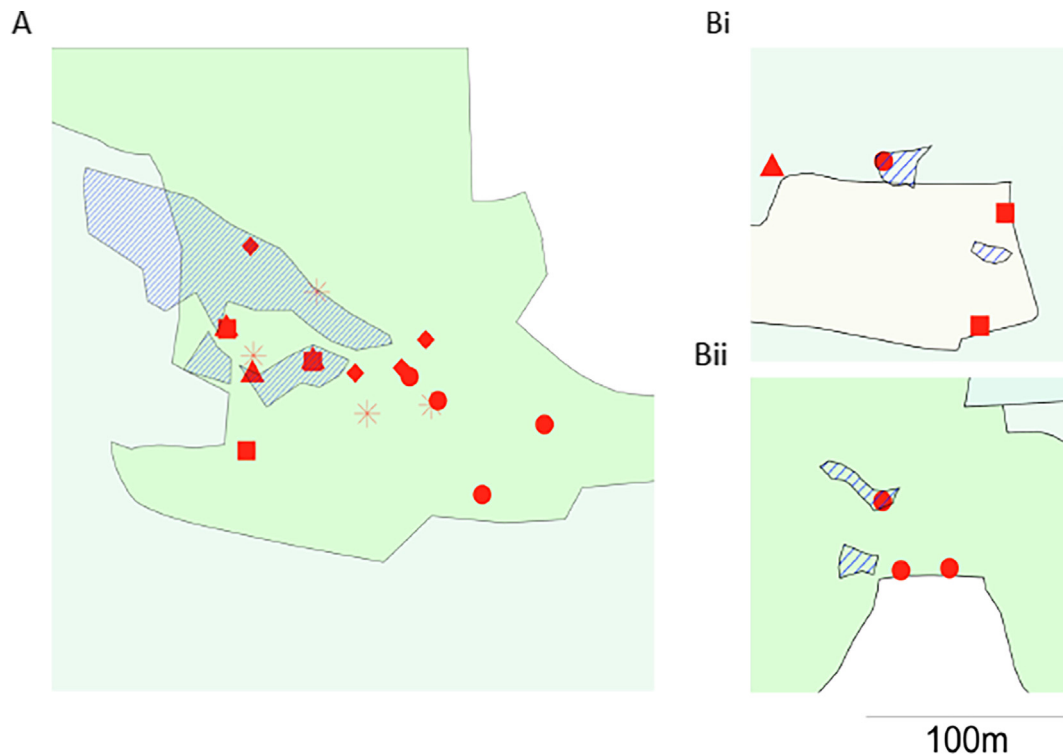


Fig. 2. Locations of daytime resting sites of dormice (red points) in areas where tree felling was carried out in (A) South Devon and (B) Central Kent. Areas where trees were completely removed are shown as hashed blue areas. Individual dormice in the different areas are shown with different symbols (circle, triangle, square and star). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Fieberg and Börger, 2012; Gitzen et al., 2006; Walter et al., 2015; Walter et al., 2011). Bivariate normal smoothing and a default grid resolution of 151×151 cells were used in kernel density estimation. The 95% contour level and 50% contour level of the KDEs were extracted as measures of the areas of total range and core range. 95% CIs were calculated for each 95% and 50% KDE with 1000 bootstrap samples with replacement.

Range size estimates had high 95% CIs, so distances travelled and centroids of ranges were also used to investigate space use and the effect of felling (Fieberg and Börger, 2012). The night-time extent of ranging was calculated as the distance between each night-time fix and the resting site the dormouse had used the previous day (Fieberg and Kochanny, 2005). The distance between centroids of KDEs calculated before and after felling were used to assess the extent to which dormice ranges had shifted (Fieberg and Kochanny, 2005). 95% CIs around centroid distances were calculated using bootstrapping with replacement to generate 1000 samples of centroids before and after felling and calculating the difference between them.

2.5. Habitat preference

The preferences of dormice for aspects of vegetation structure were investigated for night-time ranging and resting site selection in the day. We used a use-availability design (Aebischer et al., 1993; Boyce and McDonald, 1999; Warton and Aarts, 2013), comparing habitat characteristics of used locations from radio-tracking to those of available locations, determined at a set of randomly sampled locations (Aarts et al., 2013). For assessing night-time habitat preference, a set of random points was generated around each day-time resting site. Differences between the coordinates of day-time resting sites and of night-time active fixes for all dormice were calculated, and locations at these distances were randomly sampled to reflect biologically meaningful accessibility (Matthiopoulos, 2003). For every day spent at each resting site, 50 random locations were sampled. This generated an average of

204 (± 30 SE) random locations in the habitat surrounding each nesting site.

For assessing preferences for day-time resting site habitat, 100 random locations in a 100 m radius around each resting site were sampled. These were not weighted by distance, as dormice could shift their resting location up to this distance in a night. This gave an average of 886 (± 175 SE) randomly sampled locations of possible resting habitat for each dormouse.

To account for a margin of error in locating animals arising from VHF and GPS accuracy (GPS mode accuracy was 3 m), canopy variables in a 5 m radius around each randomly generated location and each location used by dormice were calculated. For the random locations, those that fell within open areas were excluded. The eight canopy variables calculated in each 5 m buffer were: variation (standard deviation) in canopy height; canopy density (proportion of vegetation heights > 4 m); local variation in canopy density (the standard deviation in canopy height of a 3×3 m sliding window around each pixel averaged within the 5 m radius around each location); and proportion of vegetation 0–1 m; 1–2 m; 2–5 m; 5–10 m; and > 10 m. Spearman's rank correlation tests were used to investigate co-linearity between these canopy variables (Zuur et al., 2010), many of which were correlated. A Principal Component Analysis (PCA) was therefore conducted for canopy variables giving a set of principal components (PCs) for each analysis (Appendix B). All PCs explaining more than 5% of variation in the data were used in analyses of vegetation structure.

Preferences of dormice for particular tree species were assessed using a similar use-availability design, with availability derived from the tree species sampled within the ranges of the dormice. Estimates of availability were calculated through bootstrapping (with replacement) the available trees 1000 times. Each sample was the same size as the number of records of trees used by each dormouse. 95% CIs for the availability of tree species was calculated for each dormouse range and aggregated across dormice (Appendix C).

2.6. Statistical analyses

All model selection (excluding tree species preference models – see below) was performed using an information-theoretic approach and the effects of explanatory variables were derived through multi-model inference via model averaging. This approach involves assessing candidate models of all possible combinations of explanatory variables and ranking these by Akaike's Information Criterion (AIC), adjusted for sample size (AICc) (Lindberg et al., 2015; Whittingham et al., 2006). These models were fitted by Maximum Likelihood for mixed effects models. The top set of models most likely to explain variation in dormouse behaviour measures were all those within 2 Δ AIC of the top model (Burnham and Anderson, 2002). Full model averaging was performed across this top model set, weighted by their relative AICc values, to calculate effect sizes of explanatory variables. Full model averaging sets effect sizes at zero when variables are not present in a model and is thus more conservative (Grueber et al., 2011). 95% Confidence intervals were calculated for effect sizes and significance was determined by whether or not these confidence intervals overlapped zero. The relative importance (RI) of each variable is defined as the proportion of models within the top model set that included that term. For models with small numbers of explanatory variables, stepwise selection was also performed and all results proved robust. In analyses where the response variable was at the level of individual dormice (e.g. dormouse ranges), site was included as an explanatory variable to account for differences between sites. In analyses where the response variable was single instances of habitat use (e.g. habitat preference), dormouse identity was included as a random or fixed factor to control for variation arising from the identity of the dormouse.

To investigate whether 95% and 50% range areas and mean distances travelled varied between dormice, a linear model with a Gaussian error structure was used with site, weight and sex as explanatory variables. Range sizes were square-root transformed and mean distances travelled were logged to normalise their distribution. The relationship between distances travelled from the daytime resting site and the hour of night and the implementation of tree felling was analysed in a generalised linear mixed model framework with dormouse identity as a random effect (Bolker et al., 2009). Distances were square-root transformed to normalise their distribution. A linear model with a Gaussian error structure was used to test for a difference between range shifts of dormice in felling treatments and non-felling controls. This model included site as a fixed term to control for site identity. Distances between range centroids before and after felling were logged to normalise their distribution.

To assess tree species preferences, generalised linear modelling with a negative binomial error structure was used to model counts of use and availability for each tree species for each dormouse. A saturated model with a three-way-interaction between used/available, tree species and dormouse ID was simplified via backwards step selection (Crawley, 2013). Whether terms explained a significant proportion of variance was determined by likelihood-ratio tests. For each dormouse, the difference between recorded use and each of 1000 bootstrap samples of tree species availability was used to calculate 95% CIs for each tree species available to each dormouse. These were then averaged across dormice for each tree species that was used by at least two dormice, and importance denoted by whether 95% CIs overlapped zero.

To analyse vegetation structure preference for day-time resting and night-time ranging, mixed effect logistic regression modelling, with a binomial error structure, logit link and random effect for dormouse identity was used (Aarts et al., 2008; Beyer et al., 2010). This was done in two ways: first, models were run with the explanatory variables as original individual scaled LiDAR variables and then second with explanatory variables as continuous, scaled principal components derived from LiDAR canopy measures. In the first method, many of these variables were correlated so model selection precluded any variable pair with correlations of > 0.6 r_s from being included together in

models. This method, however, understates the importance of variables with correlations to many others, and cannot capture the combination of intercorrelated aspects of vegetation structure that characterise woodland habitats. The explanatory variables used in our main analyses were therefore the continuous, scaled principal components derived from LiDAR canopy measures (Aarts et al., 2008; Matthiopoulos et al., 2011). The fit of logistic regression models was evaluated using repeated k-fold cross-validation procedures (Boyce et al., 2002) using code modified from the R package *hab* (Basille, 2015). The final model was fitted to a portion of the data (a 'training set') and used to predict values for the remaining data (a 'test' set). Huberty's (1994) heuristic was used to calculate the division of training and test data (Fielding and Bell, 1997). The equal-area binned distribution of the test data and predictions from the model was compared via a Spearman's Rank Correlation test (r_s ; Wiens et al., 2008). This was conducted separately for used and available habitat, and repeated 100 times. The fit of the model was assessed through r_s correlations for used habitat, and t-tests on the differences between the correlation values of used and available habitat.

3. Results

3.1. Ranging behaviour and resting sites

The number of fixes taken for each dormouse ranged from 14 to 96; those tracked for over 13 days had at least 34 fixes. After collar failure and loss, 16 dormice were tracked for 13 days or more: eight in felling areas and eight in control areas, with four males and females in each.

The mean range area used by dormice (95% KDE) over a thirteen-day period was 0.51 Ha (± 0.07 Ha SE) and the mean core area (50% KDE) was 0.09 Ha (± 0.02 Ha SE) (Fig. 3). The mean number of resting sites for each dormouse was 2.7 (± 0.3 SE, Range 1–5). The mean night-time distance ranged from the preceding resting sites was 46.3 m (± 1.3 m SE). For individual dormice, the mean distance travelled ranged from 9.5 m (± 0.4 m SE) to 61.3 m (± 3.6 m SE). 43% of resting sites were in dormouse nest boxes (25 out of 58 resting sites). The other 33 resting sites were in abandoned squirrel dreys, birds' nests, or tree hollows ($n = 21$), low shrub, e.g. bramble, or bracken ($n = 10$), a tree guard ($n = 1$) and a tree stump ($n = 1$).

Sex and site did not significantly affect the overall (95% KDE) or core (50% KDE) ranges of dormice or the mean distances they travelled from resting sites. However, heavier dormice used smaller ranges (Effect size (E_s) = -3.03 (-5.74 , -0.31 95% CIs); Relative Importance (RI) = 1) but not smaller core ranges (RI = 0.64) and travelled less far from resting sites (E_s = -0.07 (-0.11 , -0.02 95% CIs); RI = 1).

3.2. Habitat and species preferences

The Simpson's index of vegetation species diversity ranged between 0.61 and 0.89 within dormouse ranges, with a mean of 0.76 (0.20 SE). Tree species were consistently used to different extents by dormice (LR test = 50.8; $p < 0.001$, Fig. 4, Appendix C). Yew (7.24–9.75 95% CI difference between use and availability), rowan (1.00–3.00 95% CIs), and hazel (1.00–12.23 95% CIs) were especially favoured relative to availability. There were no differences among dormice in their relative use of tree species (LR test = 14.4; $p = 0.57$), however, different species of tree were available to different dormice (LR test = 57.0; $p < 0.001$).

Within dormouse ranges, the average canopy height was 8.3 m (0.5 SE) and mean canopy density was 83% (3% SE). Mean vegetation heights within dormouse ranges varied from 4.5 m to 12.1 m, while variation (standard deviation) in heights ranged from 2.7 m to 5.6 m, and canopy density from 46% to 96%.

Several aspects of vegetation structure (based on LiDAR-derived PCs) had a strong effect on whether areas were selected by dormice

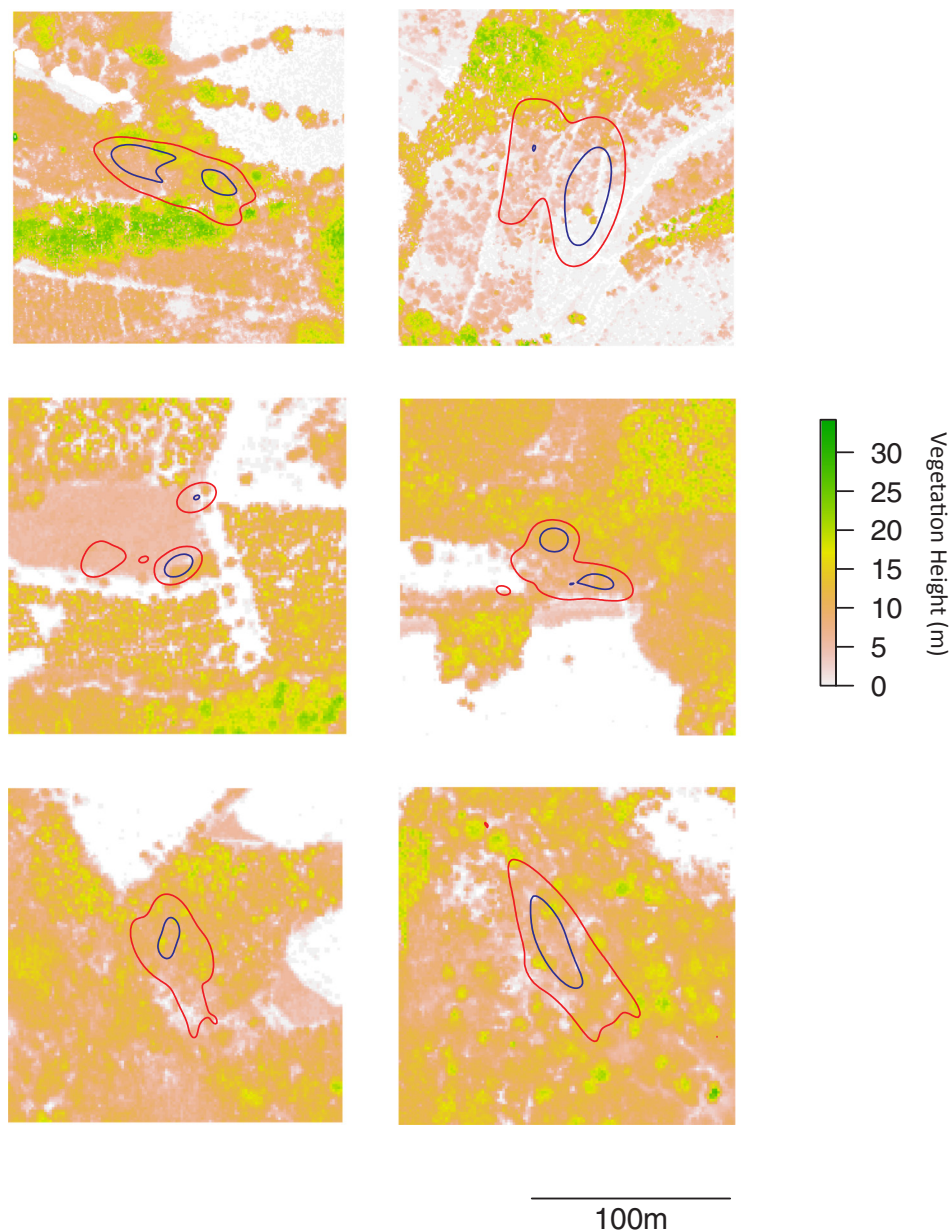


Fig. 3. Examples of radio-tracked dormouse home ranges. 95% outer contours of Kernel Density Estimates are shown in red and 50% core ranges are shown in blue. Used location records are shown by grey crosses. LiDAR vegetation structure data are also shown: colours indicate vegetation height in metres (m) and all vegetation < 0.5 m was excluded from analysis. Scale is the same in all panels.

during night-time ranging (Fig. 5). Areas selected by ranging dormice had higher canopy density and a lower proportion of vegetation heights < 5 m (LiDAR PC1); a greater proportion of 5–10 m trees, less variation in canopy height and a lower proportion of trees over 10 m (PC2); a higher proportion of 0–1 m and 5–10 m vegetation heights in conjunction with less vegetation of 2–5 m (PC4); and a higher proportion of 0–1 m vegetation in conjunction with less vegetation of 1–2 m (PC5). The fact that dormice ranged in woodland patches that contained both 0–1 m vegetation and 5–10 m vegetation within a 5 m radius represents the use of areas with both open and mid-height vegetation. These areas are therefore edge habitats, and could represent fine-scale mosaic structuring within the woodland, internal edges between woodland stands, and external woodland edges. This model fitted well and had high predictive power ($R_s = 0.83$ (0.81, 0.84 95% CIs); $p < 0.01$; Appendix D) and the R_s correlations for used habitat were much higher than for available habitat ($t_{115} = 26.2$, $p < 0.001$), signifying that the model could accurately predict whether woodland

habitat was used compared to a random sample.

Analysis of original individual LiDAR measures supported the main results for LiDAR PCs. The proportion of habitat vegetation 0–1 m ($E_s = 0.14$ (0.06, 0.22 95% CIs); $RI = 1$) and 5–10 m high ($E_s = 0.20$ (0.11, 0.29 95% CIs); $RI = 1$) were higher in areas selected by ranging dormice. The proportion of vegetation between 1 and 2 m high ($E_s = -0.25$ (-0.39, -0.11 95% CIs); $RI = 1$), and the variation in canopy height ($E_s = -0.23$ (-0.34, -0.12 95% CIs); $RI = 1$), were both lower in areas preferred by ranging dormice. The local ‘clumpiness’ of vegetation ($RI = 0.3$), and the proportion of vegetation between 2 and 5 m ($RI = 0.2$) and over 10 m ($RI = 0$) had no effect on ranging habitat selection.

The selection by dormice of habitat for daytime resting sites was also strongly affected by LiDAR-derived vegetation structure PC2 (Fig. 5). Areas selected by dormice for daytime resting had a greater proportion of 5–10 m trees, less variation in canopy height and a lower proportion of trees over 10 m. This model also had significant

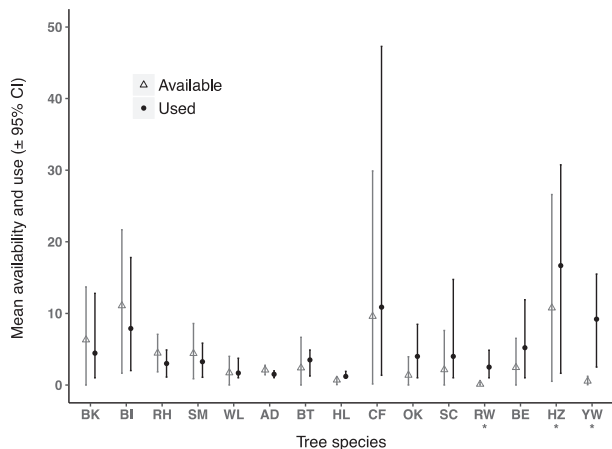


Fig. 4. The availability of tree and plant species and their use by dormice on two woodland sites in Kent and Devon, England. The mean count and 95% CIs of trees used by dormice were calculated from the locations of active, radio-tracked dormice. Species are ranked by the mean difference between their use and availability. The mean and 95% CIs of available trees were calculated from bootstrap samples of availability on transects surveyed from the centre of each dormouse's home range. Only species that were used by at least two individual dormice are shown. Species which had zero use or availability counts were excluded. BK = Bracken, BI = Birch, RH = *Rhododendron*, SM = Sycamore, WL = willow, AD = Alder, BT = Buckthorn, HL = Holly, CF = Conifer, OK = Oak, SC = Sweet Chestnut, RW = Rowan, BE = Beech, HZ = Hazel, YW = Yew. Significance of the difference between use and availability 95% CIs of species is denoted by *.

predictive power ($R_s = 0.60$ (0.57, 0.63 95% CIs); $p = < 0.05$, Appendix D), but was not as strong as the model for ranging habitat preference, and the r_s correlations for used habitats were higher than for available habitats ($t_{115} = 15.0$, $p < 0.001$). No individual original LiDAR measure was associated with day-time resting habitat selection.

3.3. Effects of felling

The distances travelled by dormice from the resting site did not differ before and after felling, or between sites with and without felling ($RI = 0.24$; Fig. 6). The ranges of dormice in areas where felling was conducted shifted to a lesser extent than those in areas where no felling was conducted ($Es = 0.81$ (0.12, 1.50 95% CIs); $RI = 1$; Fig. 7). Dormice were found in the same locations immediately before and after felling in 23 of 26 occasions. Of the three instances of movement, one dormouse

moved 35 m from a nest box surrounded by tree removal work to a small oak tree, while another individual moved 43 m between nest-boxes on two days when felling was being carried out in the vicinity.

4. Discussion

4.1. Habitat preferences of dormice

The night-time ranging habitat preferences of tracked dormice were for higher proportions of vegetation of 5–10 m, lower proportions of high forest and lower variations in canopy density. These vegetation structures have also been found to be a consistent indicator of relatively high dormouse abundance and breeding frequency at a site level (Goodwin et al., 2018), suggesting the local, individual preferences observed here can be scaled up to a population level. The positive associations of tracked dormice with low variation in canopy density reflect their selection of a particular canopy density and, although not established empirically, dormice have been reported to require habitat with high branch-connectivity between trees and shrubs in order to enable ranging and dispersal (Bright, 1998; Bright and Morris, 1994). Dormice also preferred to range near edge habitats. Dormice have been associated with woodland edge habitats through other survey methods (Berg and Berg, 1998; Bright et al., 1994; Ramakers et al., 2014) but not previously through direct observation of their ranging behaviour. There is increased light and warmth from greater insolation at woodland edges and both promote fruiting and flowering, providing food for dormice (Juškaitis, 2007).

The selection of vegetation at certain heights and densities will clearly depend on their availability (Aarts et al., 2013). Although not markedly different from our findings that dormice used canopy heights of between 5 and 10 m, Bright and Morris (1991) observed dormice to use lower tree heights of 4.14 m to 5.19 m corresponding to a lower woodland canopy height overall of 5–6 m. In very different woodland habitats, habitat preferences might therefore vary in relation to the available structures and species. Even within our study, there are differences in habitat preference based on the habitats available to each dormouse. The high predictive ability of our models, however, suggests that the habitat preferences we found are consistent between individuals (Boyce et al., 2002; Johnson et al., 2006).

Dormouse populations have been also been shown to be positively associated with a variety habitat types (Goodwin et al., 2018; Berg and Berg, 1998), some of which were likely under-represented on our study sites. Dormouse populations may be more flexible in their habitat use when more, or different, habitats are available. Furthermore,

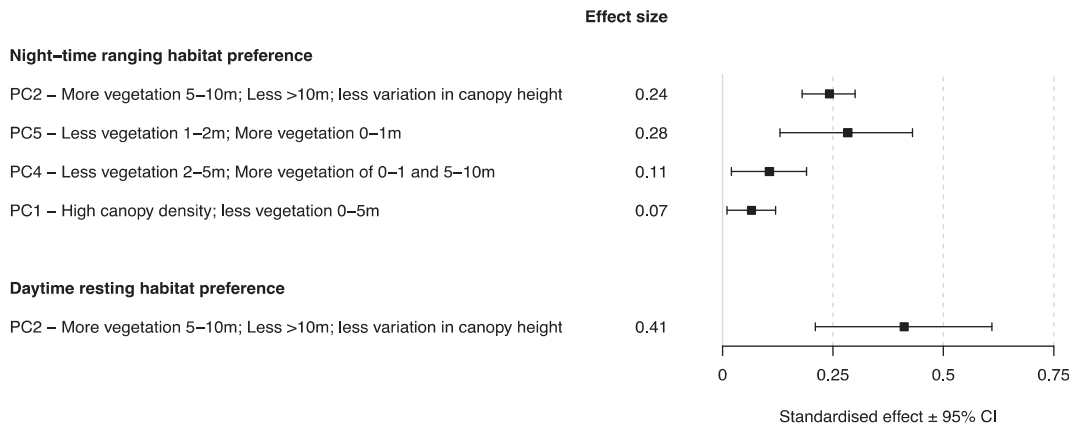


Fig. 5. Habitat preferences of radiotracked hazel dormice on sites in Kent and Devon, England. The effects of vegetation structure on the relative intensity of use are shown separately for night-time ranging and daytime resting. Vegetation structure is described by Principal Components (PCs) from analysis of LiDAR data. The standardised effect sizes (\pm 95% Confidence Intervals) are derived from mixed-effect binary logistic model averaging logit estimates of effect sizes across the top model set. Relative importance across the top model sets of all the terms shown is 1. Terms are shown in order of the strength of effect (as derived through effect size and accuracy of effect size estimation (CIs)).

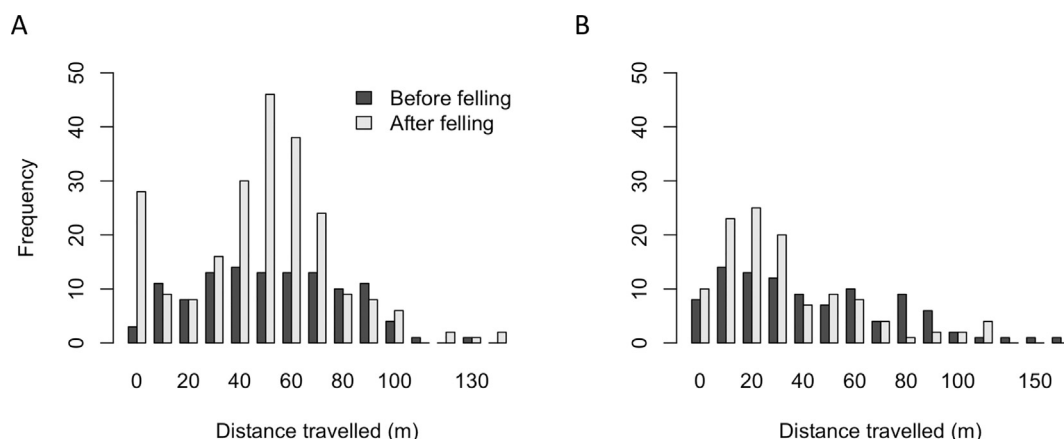


Fig. 6. The frequency at which dormice were recorded at night at different distances from their daytime resting site, before and after felling periods, in areas where felling was conducted (A) and control areas where felling was not conducted (B).

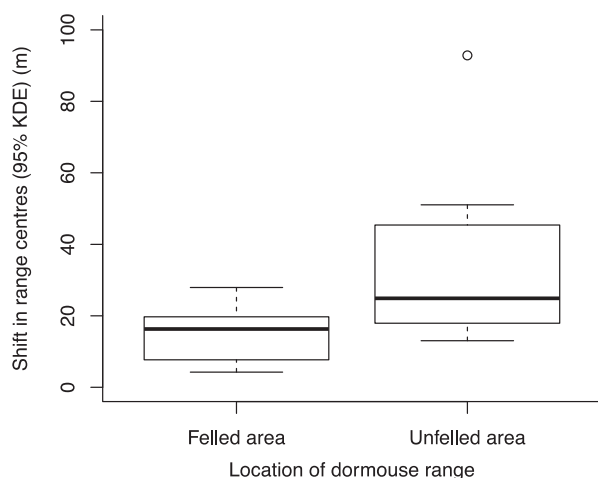


Fig. 7. A comparison of the extent of the home range shift (the distance between home range centroids calculated in pre- and post-felling periods) between radiotracked hazel dormice in areas with tree felling and areas with no tree felling. The box plot indicates the median displacement distance with the box indicating the 50% range and the whiskers indicating the 75% range in overall distances (m).

hedgerows and more woodland connections in the landscape have been found to be important for dormice (Bright et al., 1994; Goodwin et al., 2018). While we know little of the effects of variations in hedgerow habitat, these beneficial habitat features in the landscape may mitigate or affect the influence of habitat change within a woodland.

Bright and Morris (1992) found that in woodland with different vegetation layers (i.e. an understorey and canopy layer), dormice used different vegetation heights depending on the seasonal availability of food resources. Woodland in our study, however, was of one layer, either mixed, shrubby woodland or beech or conifer high woodland without an understorey, therefore dormouse activity would have predominantly been in the canopy. This cautions against applying the habitat preference findings of this work to such woodland habitats, with understorey and canopy layers. The use by dormice of different layers within woodland would have been difficult to examine using our methodology. It would be necessary to employ a tracking methodology to identify the position of dormice in a vertical dimension and to measure the vertical vegetation structure of woodlands, e.g. through the use of waveform LiDAR (Anderson et al., 2016) or terrestrial laser scanning (Eichhorn et al., 2017).

Resting site selection is in part determined by proximity to suitable ranging habitat, creating a likelihood of identifying a similar preference

for both (Guo et al., 2008). Resting sites were, however, associated with only one preferred ranging habitat, where there was more vegetation of 5–10 m, fewer high trees, and less variation in canopy heights, suggesting that these sites tended to be more in the core areas of the animals' ranges, further from edges and more likely to be protected from weather and predation (Chutipong et al., 2015; Rader and Krockenberger, 2006). Dormouse preference for nest sites within woodland interiors is supported by other studies (Williams et al., 2013).

While dormouse resting site preference may be for areas with a higher proportion of 5–10 m trees, actual dormouse nests were often situated in features associated with old growth; 67% of natural dormouse nests (38% of all nests) were in tree cavities or squirrel dreys and birds' nests in mature trees. This creates a necessity to preserve mature trees and old-growth features in order to provide adequate nesting sites, particularly in woodlands with less bramble and other dense shrub habitat (as also found by Hurrell and McIntosh, 1984).

The preferences of dormice for particular tree species can guide management, though their value and preferences will clearly change seasonally as species produce flowers, fruit and seeds and their insect populations fluctuate (Bright and Morris, 1992). Preferences for hazel and yew shown by dormice in this study are consistent with the work of Bright and Morris (1993), in which yew was preferred in late summer, while hazel was preferred in early autumn. Bright and Morris (1993) also identified preferences for honeysuckle which we did not replicate here. The use of climbing species, such as honeysuckle, may be generally under-recorded, as its use cannot strictly be distinguished from that of the tree in which it is climbing. Otherwise, discrepancies between our study and the earlier work likely arise from differences in species composition among sites. Rowan, which we found to be preferred by dormice, was not present on the study sites of Bright and Morris (1993), but is similar to other soft-masting trees they identified, such as wayfaring tree *Viburnum lantana*.

4.2. Effects of tree-felling

Perhaps counterintuitively, dormice living adjacent to felled areas shifted their ranges to a lesser extent than dormice in non-felled areas. This reduction in resting site mobility could represent a 'hiding' response (Escobar et al., 2015), perhaps associated with a perception of increased risk arising from the noise and habitat change caused by forestry operations. However, the nightly distances travelled by dormice after felling did not differ, suggesting that dormice movement was not substantially restricted within their range. Rather, we suggest the ability or willingness for dormice to disperse to other resting or ranging habitats was reduced. This might be due to felling reducing either connectivity and/or the availability of nest sites in the surroundings

(Spring et al., 2008). Habitat change may have particularly prominent effects on individual dormice due to their small range size. Dormouse ranges in these woodlands were small but consistent with other studies, even considering the variable lengths of time for which dormice were tracked (Bright and Morris, 1992, 1991). Sensitivity to habitat connectivity has also been identified at larger scales, where fragmentation leads to reduced dispersal of dormice (Buchner, 2008; Mortelliti et al., 2013).

Tree removal in this study was small-scale and was oriented towards woodland conservation. Felling practices are, however, very variable. Commercial felling affects wide areas leading to more vegetation disturbance, habitat loss and fragmentation (Bogdziewicz and Zwolak, 2014; Trout et al., 2012), with likely greater consequences for dormouse survival and emigration (Connette and Semlitsch, 2015; Escobar et al., 2015). Experimental manipulation of forestry intensity and practices (e.g. the % of canopy removed) is challenging to implement in a real-world forestry context, however experiments would help guide recommendations for forestry and woodland management practise. Although in the UK, under the Forestry Act, there is a stipulation that forests and woodlands must be re-created and so the loss and fragmentation of woodland is, in principle at least, of short duration. The noise and disturbance of even small-scale felling is considerable; in our study chainsaws were used directly adjacent to occupied nest boxes. Perhaps surprisingly, the majority of dormice did not flee from this disturbance, suggesting that large-scale, contiguous felling could have impacts on dormouse survival (Blumstein, 2010; Escobar et al., 2015). In addition, at other times of year dormice are often in torpor during the day and so might be more vulnerable to felling events. From this study, however, we cannot determine the effects of more direct physical disturbance to the resting sites of dormice (such as that caused by a large number of falling trees). It is possible that more direct disturbance would elicit a fleeing response in dormice. Further research into the behavioural responses exhibited by dormice to different degrees of noise and physical disturbance would be useful in predicting their response to large-scale felling.

Woodland management leads to immediate changes in vegetation structure and species composition, affecting individual animal range quality (Guo et al., 2008), though populations might nonetheless be resilient over the longer term (Converse et al., 2006). Studies have found little effect of management interventions in parts of a woodland on the abundance of dormice across the entire woodland (Juškaitis, 2008; Trout et al., 2012). Negative effects of habitat alteration for dormice in the short term may be offset by immigration and increases in survival once succession progresses and habitats rapidly become suitable (Juškaitis, 2008; Sozio et al., 2016). In fact, some forms of felling, such as thinning and Continuous Cover Forestry, can increase habitat suitability in the longer term by creating glades, a more open canopy (Berg and Berg, 1998; Juškaitis and Šiožinyte, 2008; Goodwin et al., 2018), and over time the dense, mid-height vegetation and edge habitats which ranging dormice prefer.

4.3. Implications for woodland management and dormouse conservation

The promotion and preservation of mid-height trees of 5–10 m and edge habitats, and reductions in high forest will increase the provision of resting and ranging habitats for dormice, although old growth features should also be retained to provide adequate nesting opportunities. Maintaining a dense, highly connected layer between trees will also allow for increased ranging movements. Preserving yew, rowan and hazel trees will also provide preferred autumn habitats for dormice. As dormouse range sizes are small and may lack the flexibility to encompass more resources where required, preferred food plants should be distributed across woodlands to increase their carrying capacity and population abundance.

The lack of behavioural response of dormice to tree removal work could have implications for reduced survival of individual dormice.

These effects could be mitigated by the scale of patch removal and the maintenance of some connectivity (Lemkuhl et al., 2006). However, dormouse preferences for mid-height, scrubby habitats that arise shortly after felling and clearance, emphasise the need for active management to maintain their preferred habitats. Therefore, management will need to find an optimum between felling, which is essential for both silvicultural purposes and for dormouse conservation, and the creation and maintenance of dense and productive understorey, while retaining old growth features. This will inevitably include a trade-off between the likely short-term negative consequences of forestry operations for individual dormice and the long-term positive effects of management for dormouse populations.

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Appendix A. Supplementary material

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